Size-dependant strategies in response to drought by *Neochanna burrowsius*

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Abstract

Canterbury mudfish (*Neochanna burrowsius*) occur in drought prone habitats and exhibit behavioural responses that are likely to enhance drought survival. This study investigated whether deteriorating environmental conditions apply size-dependent constraints on *N. burrowsius*, leading to differing behavioural strategies of survival. During a drought, numerous *N. burrowsius* were discovered in a subterranean cavity in an area that had desiccated. Mortality of these emersed fish was substantial and was dependent on substratum characteristics. *Neochanna burrowsius* were also still present in an adjacent remnant pool. There were significant differences in the sizes of fish successfully adopting the differing strategies of immersion and emersion. These results suggest that larger fish may actively leave the water and find refuge, leaving smaller fish still immersed in remnant pools. This field-based study supports laboratory studies and physiological theory that have emphasised the importance of size in determining the affects of drought on fish.

Keywords: *Neochanna burrowsius* - Canterbury mudfish - Galaxiidae - drought - refuge - size-dependent.

Introduction

Droughts develop slowly, with aquatic habitat advancing through a process of flow cessation, progressive hypoxia and finally, habitat desiccation (Lake 2000). Canterbury mudfish (*Neochanna burrowsius*), the focus of this study, occur in drought prone habitats and exhibit behavioural responses that are likely to enhance drought survival (Eldon 1979a). In the laboratory, three behavioural responses to hypoxia were observed in *N. burrowsius* by Meredith (1981). In his study, most fish rose to the water surface, took and held an air bubble in their buccal cavity, then either returned to the bottom of the tank, or remained at the water surface with the air bubble providing buoyancy. A further behaviour was for fish to attempt to leave the hypoxic water immediately, without establishing a pattern of air breathing (Meredith 1981). These behaviours indicate that *N. burrowsius* exhibit a variety of responses to hypoxia in the laboratory. In this study,

I investigated the response of *N. burrowsius* to drought in a field situation. Specifically, whether deteriorating environmental conditions apply size-dependent constraints on *N. burrowsius*, leading to differing behavioural strategies of drought survival.

Neochanna burrowsius show an ability to survive without water (emersion) for a considerable period, likely to be between one and five months (Eldon *et al.* 1978; Meredith 1985). In general, *N. burrowsius* is able to survive emersion because of a low metabolic rate, cutaneous respiration, and considerable tolerance of homeostasis imbalance (Meredith 1985). Such amphibious adaptations, coupled with high vagility and fecundity, may facilitate persistence in drought prone habitats (Eldon *et al.* 1978; Meredith 1985; Poff & Ward 1989). However, *N. burrowsius* can also suffer substantial mortality, with drought disturbance capable of drastically reducing *N. burrowsius* populations (Eldon *et al.* 1978). Disturbance can leave a lasting imprint on community composition, population-structure, and species traits (Smale & Rabeni 1995). This is because differences in the nature and intensity of disturbance can impart differential mortality risk related to the size and behavioural response of individuals. To explain the generally small size of *Neochanna* species, Meredith (1985) proposed the concept of optimal survival size, based on constraints imposed by drought. He suggested the presence of an upper and lower size limit that would determine survival success. This idea was based on physiological constraints related to body size, which have ecological consequences for fish experiencing progressive hypoxia and emersion. For example, size influences energy reserves, because there is a negative relationship between body size and metabolic rate (Cargnelli & Gross 1997). Further, the surface area to volume ratio of fish controls the efficiency of oxygen absorption through the skin and the rate of desiccation. Thus, smaller fish are expected to be more tolerant of hypoxic conditions, whereas larger fish are likely able to survive emersion for longer periods (Burleson *et al.* 2001).

Methods

This study was conducted at Hororata Spring, Mid Canterbury (NZMS 260 L36 Rakaia 2432200E, 5735100N). Hororata Spring is a wetland complex of scour holes, spring-fed pools and slowly flowing streams. Water emanates from groundwater springs that are linked to the underlying aquifer and the Hororata River. The Hororata River is a tributary of the Selwyn River, which itself flows into Lake Ellesmere. During May 2001, Hororata Spring was extremely dry, with only small remnant pools remaining. During this period the Canterbury Plains only received 40 – 70% of its average annual rainfall, and in some places the lowest ever rainfall was recorded (Aitchison-Earl *et al.* 2001). This situation provided the opportunity to compare the size and condition of emersed fish in a dry habitat area, with fish still immersed in a remnant pool with water. The location where emersed fish were found was connected to the deep permanent pool during high flows. In this study, the permanent pool was named Spring Pool and the ephemeral pool the Confluence. At the time of sampling there was approximately 10 m of dry habitat separating the Spring Pool and the lowest point of the Confluence, where emersed fish were found. To collect fish, the

permanent Spring Pool was electrofished, whereas emersed *N. burrowsius* were excavated by hand from a discrete area.

Live fish were anesthetised, measured, weighed, and returned to habitat where they were found. Live *N. burrowsius* found in subterranean refuge were replaced, covered with cobbles, and water poured over the area to replace any lost moisture. Dead fish were measured where possible and preserved in 70% ethanol. Dissolved oxygen (measured with an YSI Model 95 DO meter) of the water present was recorded. Relative condition (Kn) was calculated using the power equation of the length – weight relationship obtained from immersed and emersed fish combined, and applied to each fish using the equation

$$Kn = Weight / 2.0^{-6} Length^{3.23}$$

When comparing relative conditions, a Kn value of 1 signifies a fish with average condition (Anderson & Gutreuter 1983). Differences in logarithmically-transformed data of length and relative condition between fish were tested by ANOVA using Statistica 6.0 (Statsoft 2001).

Results

A large number of *N. burrowsius* (>100) were found below the substratum surface of the dry Confluence habitat in May 2001. Although many *N. burrowsius* were in fine sediment within the interstitial spaces of cobbles, most were in a single large chamber approximately 40 cm below the substratum surface (refer to O'Brien [2005] for photographs). The discovery was made after a small crack in the mud, at the base of a stream bank was located. This area was excavated by hand removing substratum creating a hole 55 x 36 cm, to a depth of 52 cm. The excavated substratum was moist and the large chamber was 10 cm above the water table. This groundwater had a temperature of 12.2 °C and contained 2.9 mg l^{-1} dissolved oxygen.

Live, emersed *N. burrowsius* in this chamber reacted when disturbed, especially the smaller fish, however some were very sluggish. Many were lying on their dorsal surface, assuming a position previously described by Meredith (1985). Innumerable *N. burrowsius* skeletons were also in the chamber, forming a mass of scattered bones. This implied multi-year use as it was unlikely, considering the state of their decomposition, that so many skeletons could accumulate in one season. However, some fish appeared recently dead, being partially decomposed and covered with very small fly maggots. These flies must have followed the fish underground and were also noted by Eldon *et al.* (1978) in a similar situation. These recently dead fish were not desiccated and it is possible that the activity of the maggots could have hastened the mortality of the immobile fish.

During excavation of the chamber, *N. burrowsius* were found 15 – 42 cm below the substratum surface. Mortality appeared related to the depth and substrate type these *N. burrowsius* were found in. Of the *N. burrowsius* found between 15 – 26 cm deep in predominantly cobble and silt substratum, 65 were alive and three dead. Below this depth, a distinct dark horizon of clay was present and *N. burrowsius* showed higher mortality (24 alive, 31 dead) than in sandy deposits below (15 alive, 4 dead). Mortality rate was not

independent of location and substratum type ($x^2 = 42.3$, df = 5, $P < 0.001$). Thus, characteristics of the underlying substratum affected the mortality of *N. burrowsius* during emersion.

The length and weight of 65 *N. burrowsius* captured in the permanent Spring Pool and 104 live fish found emersed were measured. Of the dead emersed fish, 28 were sufficiently intact to allow measurement of their length. There was a significant difference (ANOVA: $F_{(2, 194)} = 17.85$, $P < 0.001$) between the lengths of emersed and immersed *N. burrowsius* (Figure 1), with *N. burrowsius* found emersed in the Confluence being significantly longer than fish found freely swimming in the adjacent Spring Pool. Fish that had emersed themselves, but had suffered mortality, were significantly shorter than emersed fish which were still alive when found. Thus, it appears that there is an upper limit to the size of fish capable of remaining immersed and a lower size-limit related to the ability to survive emersion. Generally, *N. burrowsius* >50 mm total length successfully adopted a strategy of emersion and *N. burrowsius* shorter than this remained immersed.

Emersed fish had the same mean relative body condition (Kn) as free swimming immersed fish (ANOVA: $F_{(1, 167)} = 0.013$, $P = 0.91$, mean for both groups, Kn = 0.89), which indicates that many fish in both situations had generally poor condition. However, the relative condition of emersed fish was less variable (range = 1.3 – 0.43, SE = 0.03) compared with free swimming immersed fish (range = 1.97 – 0.35, SE = 0.07).

Figure 1. Length (mean ± 1 SE) of *Neochanna burrowsius* employing differing strategies during a drought. Emersed fish were found alive, buried in sediment at the base of a stream bank. Desiccated fish were found emersed but dead in the same situation. Immersed fish were live fish electrofished from an adjacent pool of water. Different letters indicate significant differences as determined by Tukey *post hoc* tests.

Discussion

A distinctive specialisation of *Neochanna* species is a strengthened upper jaw region of the cranium (McDowall 1997). The increased ossification and proximity of bones may be an adaptation related to burrowing behaviour, such as head probing. Tasmanian mudfish (*Neochanna cleaveri*) created progressively complex burrows, first vertically and then horizontally, as water was slowly lowered in an aquarium (Koehn & Raadik 1991). Indeed, the occurrence of *N. burrowsius* in burrows, chambers and cavities has been well-documented (Phillipps 1926; Cadwallader 1975; Eldon 1979b). However, there is debate surrounding the ability of *N. burrowsius* to burrow. This uncertainty is primarily because fish did not attempt to avoid desiccation by burrowing, under controlled conditions, and at some sites large numbers of fish have been stranded after water levels dropped (Eldon 1979b). These conflicting observations may, in part be explained by the varying responses of fish of different sizes.

The discovery of a large subterranean chamber containing numerous *N. burrowsius* was serendipitous and such a large congregation of emersed *N. burrowsius* has not been recorded previously. Eldon *et al.* (1978) and Eldon (1979b) found emersed *N. burrowsius* only singly or in small groups. However, he found only 0.4% of the minimum estimate of the pre-drought population, indicating the possibility that refugia containing large numbers of *N. burrowsius* was not found. In the present study, although the substratum was relatively cool and moist, substantial mortality was recorded. Furthermore, mortality in emersed *N. burrowsius* was highest in a band of clay substratum. This mortality is likely due to low oxygen availability in clay, whereas, the more porous sandy substratum may permit greater oxygen diffusion. Thus, the location of refuge appears critical to survival. In this study, mortality due to drought was at least 25%, although this estimate does not include the large number of inseparable skeletons found. In a thorough study of a Mid Canterbury stream, 30% mortality of a *N. burrowsius* population occurred during drought conditions (Eldon *et al.* 1978). Furthermore, in laboratory investigations, 40% mortality occurred in *N. burrowsius* after 85 days of emersion (Meredith 1985). Thus, the strategy of emersion is risky and considerable mortality occurs when a habitat dries, even if seemingly suitable refugia is available.

During emersion, fish must cope with a progressive series of challenges including movement without water, gas exchange during emersion, toxic waste accumulation, and starvation (Meredith 1985; McPhail 1999). Since surviving emersion depends, in part, on physiological processes that are affected by an individuals size, it is not surprising that responses to drought vary according to fish size. The present study supports Meredith (1985) in his suggestions that there is an optimum size for surviving drought and indicates a likely mechanism. Importantly, there were significant differences in the sizes of fish successfully adopting the differing strategies of immersion and emersion. Results from this study indicate that larger fish may actively leave the water and find refuge, leaving smaller fish still immersed. Smaller fish are likely to remain immersed as they have lower oxygen demands, and higher hypoxia tolerance due to higher surface

area to volume ratios. Burleson *et al.* (2001) in experiments within oxygen gradient chambers found that smaller largemouth bass (*Micropterus salmoides*) had broader hypoxic tolerance levels and utilised water of lower dissolved oxygen more readily than larger conspecifics. Larger fish, on the other hand, have well developed respiratory systems and are likely to survive emersion for longer periods due to lower metabolic rates. For example, large bluegill (*Lepomis macrochirus*) individuals have greater condition, after winter starvation, than smaller con-specifics (Cargnelli & Gross 1997). Indeed, laboratory experiments have confirmed that during emersion, small fish lose weight much faster than larger individuals of both *N. burrowsius* and black mudfish (*Neochanna diversus*; Meredith 1985; McPhail 1999). Furthermore, small *N. diversus* showed the greatest reduction in hepatic glycogen, an important energy source, during starvation and aestivation (Davidson 1999).

Both emersion and immersion strategies are risky, however. Although immersed fish can continue to feed, they will also continue to be preyed upon by predators, which can limit the value of pools as drought refugia for small fish (Magoulick & Kobza 2003). Emersed fish, however, risk desiccation and starvation. In the present study, emersed and immersed *N. burrowsius* had the same mean relative condition, though the range of condition values varied. Meredith (1985) found that immersed, but starved *N. burrowsius*, lost weight more rapidly than emersed fish. Similar results were obtained in a laboratory study conducted on *N. diversus* (Dean 1995). Thus, remaining active represents a significant energetic cost for immersed fish. Food resources are likely to be scarce and patchy during periods of hypoxia, which may explain the large variation in condition of the immersed fish observed here. Thus, remaining immersed as a strategy for survival will be reliant on the presence of adequate food resources, which is often not the case in remnant pools during drought (Lake 2000).

In summary, the ability to use subterranean refuge is likely to have important ecological consequences for the persistence of *N. burrowsius* on the increasingly drought-stricken Canterbury Plains. During emersion, survival is dependent on microhabitat characteristics and fish may congregate each drought within a particular important refuge. However, the investigations detailed in this paper demonstrate that *N. burrowsius* of differing size employ varying survival strategies in the field. Small individuals are more likely to perish if emersed, thus their survival is dependent on the presence of remnant pools of water. This field-based study supports numerous laboratory studies and physiological theory that have emphasised the importance of size in determining the affects of drought on fish.

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